Original Article

Effect of aquatic plants upon planktonic and periphytic organisms: a microcosm-based approach

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Abstract: Aquatic plants have a major influence upon other aquatic organisms, by altering both water chemistry and spatial structure of the habitat in shallow water bodies. Some of them, such as *Stratiotes aloides* L., may suppress algal growth. But how aquatic plants would ultimately influence the heterotrophic community and the aquatic ecosystem as a whole is far from clear. Our microcosm-based study demonstrated that even a modest density of *S. aloides* caused a decline in phytoplankton chlorophyll concentration and periphytic algae abundance, including cyanobacteria, whereas diatoms appeared to be immune to the plant influence. Photosynthetic rate remained unaltered despite decreased chlorophyll concentration. While bacterial counts remained largely unchanged, more bacteria were observed forming microcolonies as well as associating with particulate organic matter. Numbers of periphytic heterotrophic organisms did not differ significantly between the planted and plant-free control microcosms. Zooplankton diversity increased and cladocerans assumed a more prominent position within the microcosms with macrophytes. We assume that the presence of plant's leads to increased importance of bacteria and protists in the functioning of the food webs. Therefore, decreasing of algal abundance does not involve reducing the number of heterotrophic planktonic and periphytic organisms.

Introduction

Aquatic plants affect water flow, cycles of organic and inorganic nutrients, water quality and aquatic community structure in the shallow waters. Macrophytes change food interaction and production of different trophic levels. Plants often reduce the abundance and generic richness of algae (Muylaert et al., 2010) and their role as primary producers. Rooney and Kalff (2003) revealed an increase in the bacterial production and violation of the classical interaction between the bacteria and phytoplankton due to the changes in the turnover of phosphorus and dissolved organic carbon caused by submerged macrophytes. As other food resources (bacteria and protozoa) are more important in the diet of zooplankton, their production may significantly exceed that of phytoplankton within stands of macrophytes (Burks et al., 2006). Aquatic plants significantly increase the amount of detritus in the aquatic ecosystems. As a result, the importance of the detritus-based food chains rises. The organic matter and energy from detritus decomposers flows to detritivores and bacteriophages, and to predators (Moore et al., 2004).

Heterotrophic organisms use aquatic plants as shelter or feeding sites. Features of the structure of heterotrophic organisms' communities within stands of macrophytes often link with the complexity of spatial structure of the habitat (McAbendroth et al., 2005). In addition, some aquatic plants can significantly alter water chemistry (Brammer and Wetzel, 1984; Pokorný et al., 1984). This aspect of the effect of macrophytes on the aquatic communities' structure has received little attention.

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We hypothesized that changes in chemical parameters of the environment caused by the vital activity of the macrophytes may influence the abundance of some species.

For our research, we have chosen water soldier (*Stratiotes aloides* L.) because this plant has a marked effect on the cationic composition of the water (Brammer and Wetzel, 1984) and has a high allelopathic potential (Burks et al., 2006). *Stratiotes aloides* is a vascular aquatic plant commonly found in the shallow mesotrophic and eutrophic water bodies. Under the right conditions, water soldier can occupy a major portion of the water body. The influence of water soldier upon planktonic and periphytic algae is well established (Jasser, 1995; Mulderij et al., 2005; Hilt, 2006; Mohamed and Al-Shehri, 2010) and is likely to alter the structure of the heterotrophic consumers' community. In the recent decades, a small number of studies looking at zooplankton community of water soldier mats (Bittel, 1980; Irvine et al., 1990; Strzałek and Koperski, 2009) and heterotrophic organisms associated with water soldier periphyton (Mieczan, 2010) have been published.

The objective of the present study was to investigate the effect of the changes in the environment (such as cationic composition and excretion of allelochemicals) caused by aquatic plants on the development of plankton and periphyton.

Materials and Methods

Microcosm design: Open-air microcosms were set up in square (1x1 m) shallow containers. To limit daily water temperature fluctuations, those containers were placed in larger water-filled concrete tanks. Containers were filled with filtered water (64 μm mesh to remove of zooplankton) probably contained algae and bacteria, to the depth of 0.3 m (total volume 300 L). Microcosms were covered by netting to prevent insects, leaf litter and mollusks entrance. After zooplankton collecting, the equal amounts of its concentrations were placed into individual microcosms. *Stratiotes aloides* was

collected from the local habitats and acclimated for two weeks under the experimental conditions. In accordance with moderate density observed in the field, ten plants per microcosm were introduced a week after the addition of zooplankton (10 ind. m^{-2}). Average wet weight of an individual plant was 173 g; at the beginning of the experiment, the plants were in the flowering or early fruiting phase. Two days after plant introduction, periphyton development was monitored using microscope slides. Each treatment was done in triplicate, with plant-free microcosms as controls.

Prior to introduction of the plants, N-NO$_3$ and N-NH^4, as well as soluble reactive phosphorus (SRP) levels were measured. To avoid N limitation of plants and algae N-NO$_3$ was added to adjust N: P ratio to 30: 1, typical for mesotrophic lakes of the region (Datsenko, 2007). Those measurements were repeated after 30 days, and 0.11 mg L^{-1} N-NH$_4$ (as ammonia chloride) was added in each microcosm. During the experiment, the levels of nitrogen and phosphorus were maintained within their typical range of water soldier habitats (Tarkowska-Kukuryk, 2006; Michalska-Hejduk et al., 2009). The experiment was monitored for 60 days.

Sample collection and analysis: Water temperature and pH values were measured daily between 09:00-10:00. Every 10 days, the concentration of oxygen, major cations (Na$^+$, K$^+$, Ca^{2+}, Mg^{2+}), biochemical oxygen demand (BOD$_5$), chemical oxygen demand (COD), chlorophyll concentration, the number of bacteria, the plankton photosynthesis rate and rate of organic matter decomposition were assessed. Every five days, the microcosms were sampled for SRP and zooplankton. Once a week, one suspended slide per microcosm was sacrificed for periphyton community analysis.

Oxygen, BOD$_5$, SRP (as orthophosphate) and COD (using permanganate procedure) were measured according to Alekin et al. (1973). Major cation concentrations were determined by the use of Flapho-4 flame photometer and AAS-1 atomic absorption spectrophotometer. The chlorophyll was measured by the spectrophotometer Lambda-25

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(Perkin-Elmer) following acetone extraction (Sirenko and Kureishevich, 1982). Bacterial cells were collected on the membrane filters (pore size 0.17 μm), stained with DAPI (Porter and Feig, 1980) and counted under the epifluorescent microscope. Bacterial biomass was calculated based on cell counts and average cell size; cell density was assumed 1 g cm^{-3}. N-NH$_4$ and N-NO$_3$ was measured by the photometric procedure using Nessler's reagent and salicylic acid, respectively, at the begining and mid-experiment (Alekin et al., 1973; Cataldo et al., 1975).

The rate of plankton photosynthesis and organic matter degradation was assessed by measuring oxygen level changes in the light and dark bottles (Kuznetsov and Dubinina, 1989). Zooplankton was collected with a 0.5 L plankton sampler at 6 locations per microcosm (3 L total), fixed with formaldehyde and counted by the standard hydrobiologycal methods. Periphyton algal, protist and rotifer community makeup and the organisms' numbers were determined by direct microscopic counts on unstained unfixed suspended slides at 280X magnification. Organisms were identified to the rank of the species, but some of them only to the genus. Periphytic organisms' biomasses were calculated using dimensions and approximated geometric shape, assuming a specific gravity of 1. In order to assess the biomasses changes of zooplankton, algae and bacteria, the approximate phytoplankton biomass was calculated, based on the chlorophyll a values and applying coefficient 0.4 (Mineeva and Shchure, 2012).

Data analysis: For all figures, the mean±one standard deviation is shown (mean±SD). Taking into account the small sample size, nonparametric methods were used in data processing. The effects of *S. aloides* on the chlorophyll a, cations concentrations, zooplankton and periphyton abundance were analyzed by Friedman ANOVA (repeated measures) test. Pairwise comparisons were made using Wilcoxon test and Bonferroni corrected. Calculations were made using PAST (Hammer et al., 2001). Correlations between parameters were evaluated by

Spearman's rank correlation coefficient using STATISTICA 6.0 software package.

Results

Chemical parameters: During the first 47 days, the microcosm's water temperature averaged 24ºC in the morning and it was rising to 30-31ºC by midday. The temperature declined towards the end of the experiment, averaging 15ºC in the morning over the final 10 days. The water pH values in the control microcosms steadily increased from 8.0 to 9.3 over the experiment; in the planted microcosms, water pH remained close to neutral (7.5-7.7), increasing in the final week to 8-8.2.

The experimental microcosms have shown lower oxygen concentration (average 6.7 mg L^{-1}) compared to that of the controls (9.2 mg L^{-1}). By midday, the oxygen concentration decrease to 4.2-4.6 mg L^{-1} both in the planted and control microcosms. In the planted microcosms, waterborne oxygen concentration correlated with the water temperature (R=-0.83, P=0.042, n=7); in the controls, oxygen correlated with the pH values (R=0.93, P=0.008, n=7).

The potassium and magnesium cation concentrations in the planted microcosms were significantly lower (Friedman ANOVA: P<0.001) compared to the controls (Fig. 1). Early in the experiment, the sodium and calcium cation concentrations in the controls exceeded those of the treatments. Then the concentrations of these ions were above the control's level in the tanks with *S. aloides*. There was a negative correlation between the calcium concentration and pH in the controls (R=-0.79, P=0.033, n=7). In the planted microcosms, a positive correlation was observed between pH and sodium (R=0.86, P=0.012, n=7), and a negative between pH and magnesium (R=-0.83, P=0.022, n=7).

SRP levels over the first 40 days of the experiment were comparable between the controls and planted microcosms. Average SRP concentration in the control and treatments were 16.3 and 17.6 μgP L^{-1}, respectively. On day 44, in the
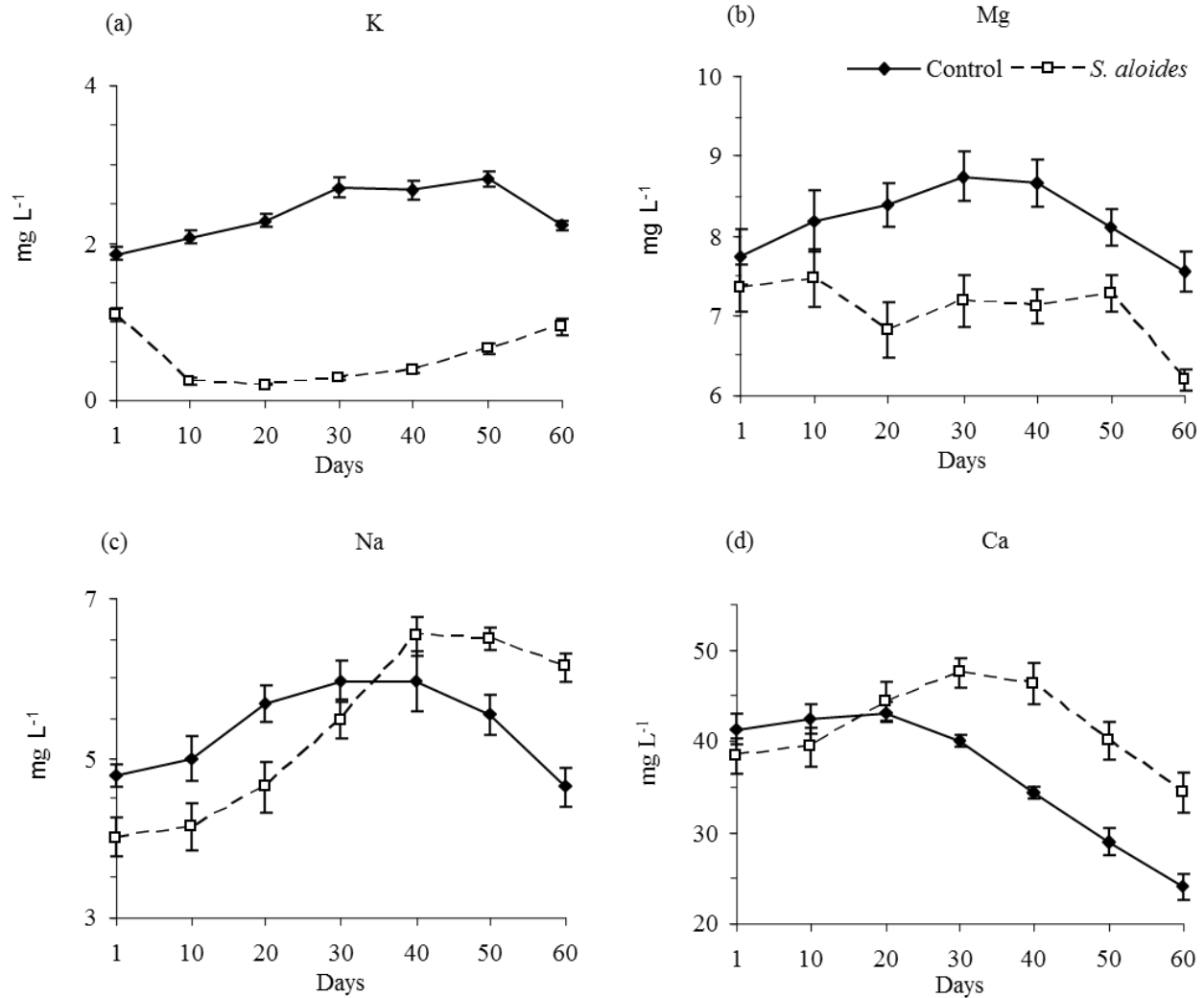
Figure 1. Cation concentrations in the experimental systems (mean±SD).

controls, SRP peaked at 50.4 μgP L^{-1}, declining to 8.3 μgP L^{-1} by day 60. In the treatments, SRP concentration steadily declined to 6.5 μgP L^{-1} from Day 44 towards the end of experiment. SRP concentration correlated with the sodium (R=0.93, P=0.008, n=6), and calcium (R=0.83, P=0.042, n=6) concentrations in the controls and treatments, respectively.

Prior to adjustment of the N:P ratio, the initial levels of waterborne nitrogen in the microcosms were 0.009 mg L^{-1} N-NO$_3$ and 0.14 L^{-1} N-NH$_4$. After 30 days, the controls contained 0.023 mg L^{-1} N-NO$_3$ and 0.13 mg L^{-1} N-NH$_4$; while the planted microcosms contained 0.013 mg L^{-1} N-NO$_3$ and 0.19 mg L^{-1} N-NH4, at which point N:P ratio was adjusted again.

BOD$_5$ and COD of the planted microcosms were two fold of those of the controls in the beginning and at the end of the experiment. At other times, BOD$_5$ and COD values in the former were below or insignificantly different from the controls. Average BOD$_5$ values over the entire experiment were similar in the controls and treatments (2.2 mg L^{-1}), ranging from 1.3 to 3.5 and 1.7 to 2.8 mg L^{-1}, respectively. COD values averaged 10.1 mg L^{-1} (ranging from 4.5 to 15.9 mg L^{-1}) and 11.1 mg L^{-1} (4.0-15.5 mg L^{-1}) in the controls and treatments, respectively. BOD$_5$ to COD ratio throughout the experiment was below 0.5, suggesting that much of the organic matter present in the system is made up of recalcitrant compounds. BOD$_5$ correlated with the phytoplankton photo-synthesis rate (R=0.93, p=0.008, n=6) in the
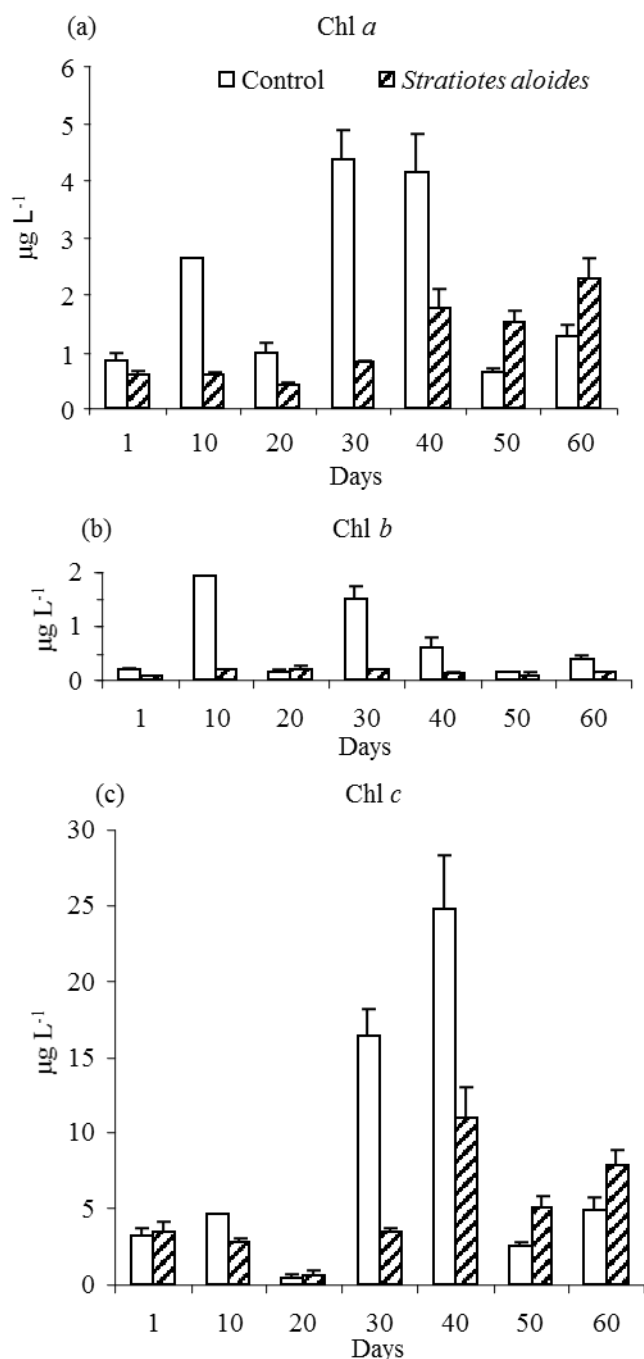
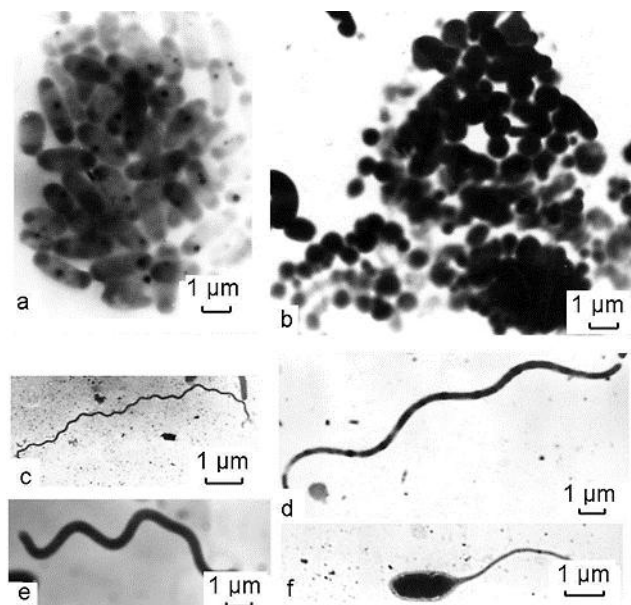Figure 2. Chlorophyll a, b and c concentrations (mean±SD).

Figure 3. Bacterial aggregates (a and b) and various bacterial morphologies (c–f) from the planted microcosms.

controls. The differences in the chlorophyll α concentration between the planted microcosms and plant-free controls were statistically significant (Friedman ANOVA: $P<0.05$). Despite two to three-fold lower chlorophyll concentrations in the treatments, the planktonic photosynthetic rates were about 0.5 mg $O_2 \cdot L^{-1} \cdot d^{-1}$ in both the treatments and controls. Photosynthesis correlated with SRP levels in the controls ($R=0.84$, $P=0.036$, $n=6$). No significant correlations between the photosynthesis rate and other measured parameters were detected in the planted microcosms.

E_{480}/E_{664} ratio stayed below 1.4, averaging 0.75 and 0.67 in the controls and planted microcosms, suggesting that the phytoplankton was not nitrogen limited (Watson and Osborne, 1979).

Bacteria: Bacterial counts were comparable in the planted microcosms and controls. Bacterial numbers and biomass averaged 5×10^6 cells mL^{-1} (ranging 3.4-7.7×10^6 cells mL^{-1}), and 0.7 mg L^{-1} (ranging 0.4-1.0 mg L^{-1}), respectively. In the planted microcosms, most bacteria were associated with detritus particles or formed micro aggregates (Fig. 3a, b). The bacterial community was dominated by small rods until 30th days and with other forms appearing by the end of the experimental period (Fig. 3c-f). In the planted microcosms, the bacterial numbers and

controls; no such correlation was observed in the planted microcosms.

Phytoplankton: Over the first 40 days of the experiment, lower concentrations of chlorophylls α, *b* and *c* were observed in the water of planted microcosms compared to controls (Fig. 2). After 50 days, the chlorophyll α and *c* concentrations increased in the treatments and declined in the
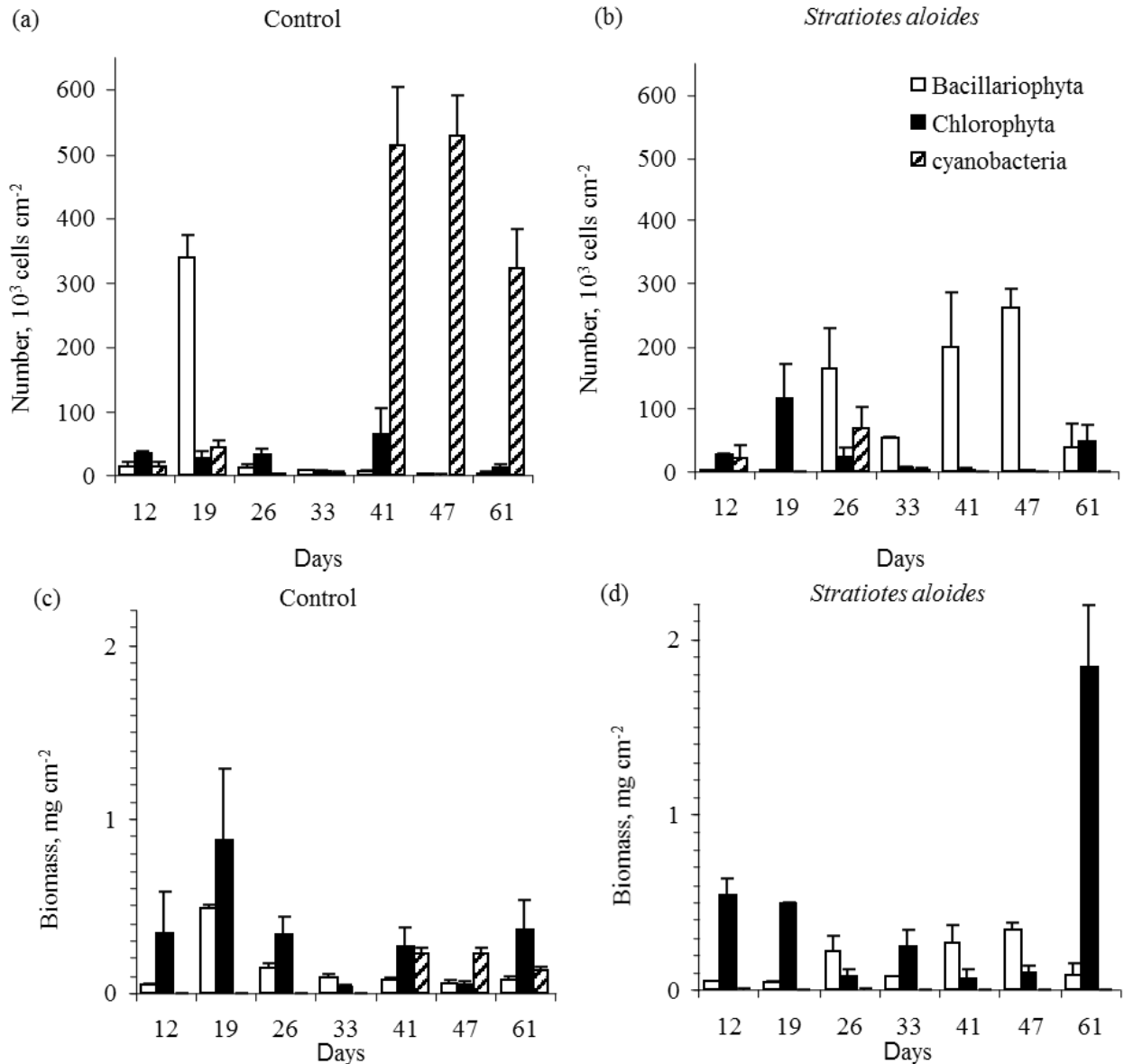
Figure 4. Periphytic algal number (a, b) and biomass (c, d) in controls and planted microcosms (mean±SD).

biomass correlated with the biomass of copepods (R=0.79, P=0.036, n=7 and R=0.86, P=0.014, n=7, respectively) and with the decomposition rates of organic matter (R=-0.79, P=0.036, n=7). Unlike bacterial counts, peaks of the organic matter decomposition coincided in the planted microcosms and controls. The rate of organic matter decomposition over the whole period of the experiment was 0.31±0.07 and 0.35±0.05 mg $O_2 \cdot L^{-1} \cdot d^{-1}$ in the controls and planted microcosms, respectively. The rate of planktonic production exceeded the rate of organic matter decomposition by a factor of 1.7 and 2 in the controls and planted microcosms,

respectively.

Microperiphyton: Submerged slides revealed the presence of algae from Bacillariophyta, Chlorophyta and Chrysophyta divisions, cyanobacteria, protists from Sarcomastigophora and Ciliophora phyla, as well as rotifers.

Algal cell numbers and biomass in the controls were ranged 18-585×10^3 cells cm^{-2} (Fig. 4a), and 0.12-1.36 mg cm^{-2}, respectively (Fig. 4c). The total number of species was 4-11. At the beginning of the experiment, in the control, the periphytic community was dominated by the green algae (*Coleochaete scutata* Brebisson, *Hormidium* sp.) and cyano-
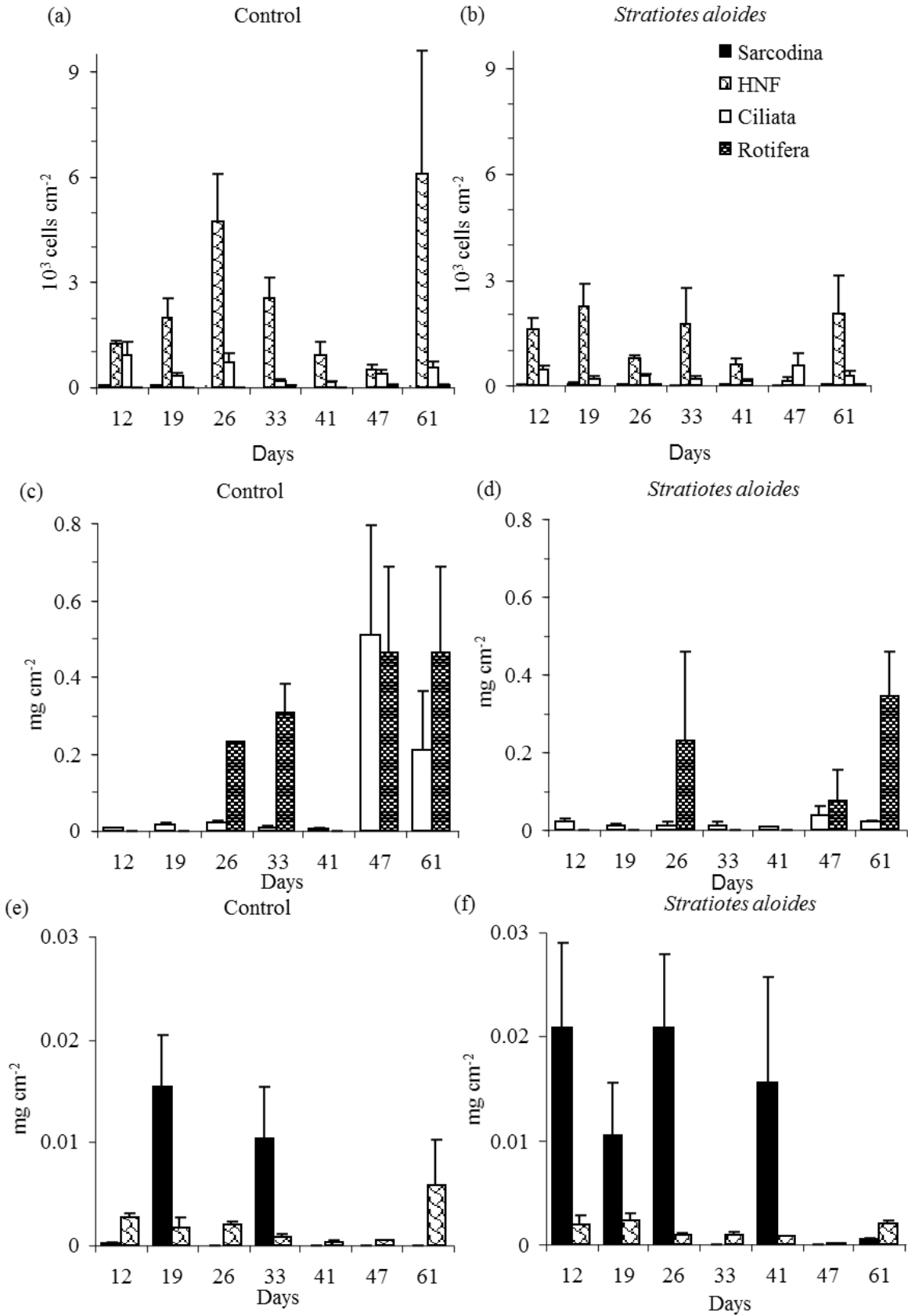
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Figure 5. Periphytic heterotrophic organisms abundance (a, b), biomass of rotifers and ciliates (c, d) and biomass of Sarcomastigophora (e, f) in controls and planted microcosms (mean±SD).

bacteria (*Aphanizomenon flos-aquae* (L.) Ralfs ex Born. et Flah). *Navicula pupula* Kütz. var. *pupula* (Fig. 4a) was the dominant species in number at 19th day, but *C. scutata* and *Synedra ulna* (Nitzsch.) Ehr. var. *ulna* contributed significantly to the biomass as well. In the second half of the experiment, the algal community was dominated by *Rivularia* sp. cyanobacteria.

In the planted microcosms, algal cell number and biomass were from $49\text{-}265\times10^3$ cells cm^{-2} (Fig. 4b) and 0.3-0.6 mg cm^{-2}, respectively during 47 days and the algal biomass peaked to 1.92 mg cm^{-2} on 60th day (Fig. 4d). Normally, 8 to 11 species of the algae were found on the submerged slides of the treatments, except during 33-47 days, when only 3 to 4 species were detected. At the early stages of the experiment, *C. scutata*, *Stigeoclonium* sp. and *A. flos-aquae* were detected in the periphytic community in the planted microcosms. Coinciding with 26th day, diatoms, especially *N. pupula*, along with *S. ulna* and *Cocconeis placentula* Her. var. *placentula* dominated the algal community, with increase of *C. scutata* by the end of experiment.

The number and biomass of cyanobacteria differed significantly (Friedman ANOVA: P<0.01) between the planted microcosms and plant-free controls. The differences in diatoms were not statistically significant (Friedman ANOVA: P=0.09).

Heterotrophic organism numbers were somewhat lower in the planted microcosms compared to controls (Fig. 5a, b); the differences were not statistically significant (Friedman ANOVA: P=0.06). They were $0.7\text{-}2.5\times10^3$ ind. cm^{-2} in the treatments and $0.9\text{-}6.7\times10^3$ ind. cm^{-2} in controls. The biomass of heterotrophic periphytic organisms ranged 0.014-0.37 mg cm^{-2} and 0.006-0.97 mg cm^{-2} in the planted microcosms and controls, respectively (Fig. 5c-f). The biomass of the most abundant organism represented by heterotrophic nanoflagellates (HNF), was very low. The most numerous organisms were *Desmarella irregularis* Stokes, *Codonosiga botrytis* (Ehrenberg) Kent, *Bodo saltans* Ehrenberg and *Anthophisa vegetans*

(O.F.M.) Stein. Ciliates were present in small numbers, but their biomass in the controls was noticeable at the end of the experiment. In the controls, the ciliate community was dominated by sedentary genera of *Vorticella* Ehrenberg, *Vaginicola* Lamarck et Ehrenberg and *Stentor polymorphus* Müller. In the planted microcosms, peak ciliate numbers were reached on 47th day, with *Vorticella* sp. and *Chilodonella uncinata* Ehrenberg present. Rotifers were *Philodina acuticornis* Murray and *Ph. citrina* Ehrenberg both in the planted and controls microcosms.

Zooplankton: A total of 48 species of zooplankton were found in this experiment; 34 of them were common in both the planted microcosms and controls. Diversity Shannon' index values calculated on the base of both numbers of individuals and biomass, were more than 50% higher in the plant-containing microcosms during 35 to 50 days.

On average, the zooplankton numbers and biomass were 86 ind. L^{-1} and 2.7 mg L^{-1} in the planted microcosms vs. 70 ind. L^{-1} and 2 mg L^{-1} in the controls. The portion of the cladocerans was greater in the planted microcosms (91% of total biomass), compared to that of the control one (79%). *Daphnia longispina* O.F. Müller was the dominant species in both control and planted microcosms (Fig. 6a). At the beginning 10th day, *Alona rectangula* Sars, (Chydoridae) found in greater numbers in the planted microcosms (Fig. 6b). In addition, *Alonella exigua* (Lillijeborg), *Graptoleberis testudinaria* (Fischer) and *Chydorus sphaericus* (O.F. Müller) were observed in appreciable numbers. Numbers of Chydoridae correlated with the numbers of periphytic HNF (R=-0.94, P=0.005, n=6). Since 40th day, substantial (up to 47 ind. L^{-1}) numbers of *Ceriodaphnia quadrangula* (O.F. Müller) was observed in the planted microcosms (Fig. 6c); those numbers were significantly higher compared to the controls (Friedman ANOVA: P<0.001). *Ceriodaphnia quadrangula* counts correlated with water pH values (R=0.87, P=0.001, n=7), sodium ion (R=0.9, P=0.00002, n=7) and chlorophyll a (R=0.77, P=0.04, n=7) concentrations.
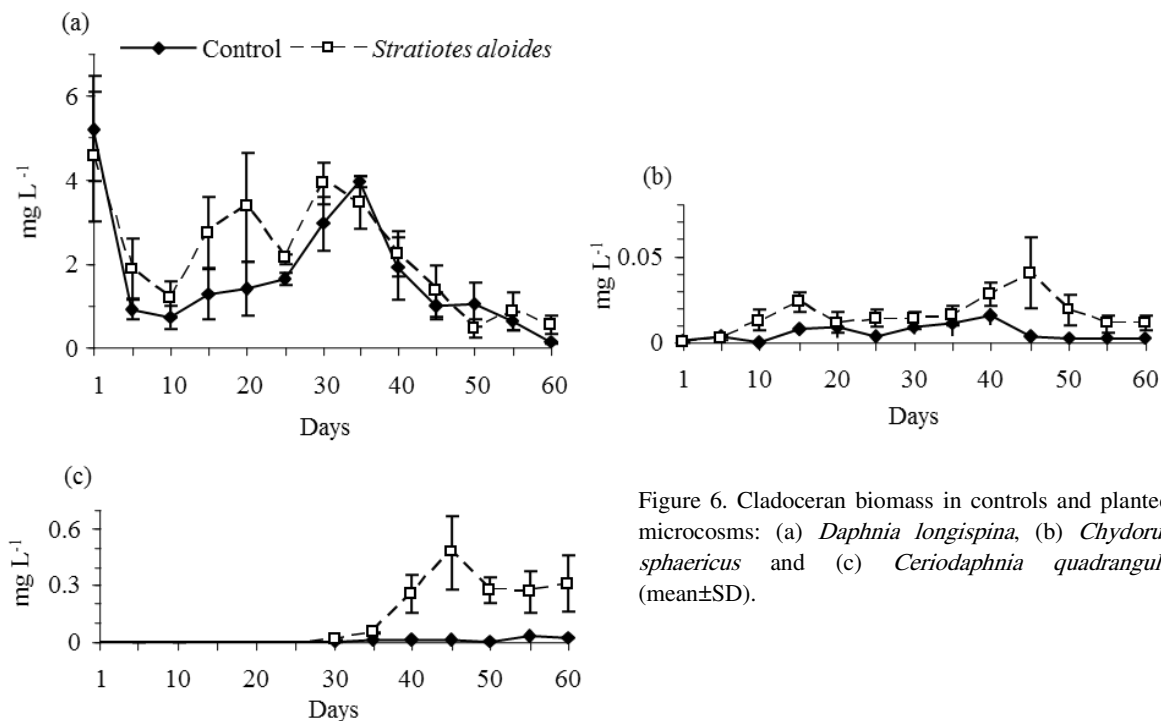
Figure 6. Cladoceran biomass in controls and planted microcosms: (a) *Daphnia longispina*, (b) *Chydorus sphaericus* and (c) *Ceriodaphnia quadrangula* (mean±SD).

Copepods averaged 30 ind. L^{-1} in both controls and planted microcosms; however, the biomass was 0.33 mg L^{-1} in the former and 0.23 mg L^{-1} in the latter. In both the controls and treatments, the vast majority of copepod numbers was represented by the juvenile stages of Cyclopoidae, whereas much of the biomass was made up by the adult and copepodite stages of Calanoidae (*Eudiaptomus gracilis* (Sars), *E. graciloides* (Lillijeborg), *Acanthodiaptomus denticornis* Wierzejski). Overall pattern of Calanoidae copepodite dynamics was similar in the controls and planted microcosms, with lower numbers in the latter (Friedman ANOVA: P<0.01). Copepod numbers reversely correlated with potassium ion concentration (R=-0.79, P=0.036, n=7) in the treatments. This relationship was not found in the controls.

Biomass of rotifers were low in the controls (approx. 0.0006 mg L^{-1}) and planted microcosms (approx. 0.0011 mg L^{-1}). The higher species richness was observed in the planted microcosms (22 species vs. 13 in the control). *Lecane luna* (Müller), *Polyarthra vulgaris* Carlin, *Keratella cochlearis* (Gosse) and *K. quadrata* (Müller) were found in both the controls and planted microcosms; *Lecane* (M.)

bulla (Gosse), *L.* (M.) *arcuata* (Bryce), *L.* (M.) *lunaris* (Ehrenberg), *Colurella obtuse* (Gosse) and *Testudinella patina* (Hermann) were only present in the planted microcosms.

Predatory zooplankters (adult Cyclopoida and *Polyphemus pediculus* (L.)) represented about 1% and 2% of the total zooplankton numbers in the controls and planted microcosms respectively.

Discussion

Algal community exhibited the most prominent response to inclusion of water soldier plants in the microcosms. The presence of macrophytes caused declining the planktonic chlorophyll levels, reduction in periphyton abundance and changes in the algal community. Macrophytes may directly influence the algae by shading, altering water chemistry, competing for nutrients, and allelopathic action or indirectly, by influencing consumers. None of the above mechanisms was identified as the dominant one.

Water soldier is known to absorb and accumulate potassium ion (Brammer and Wetzel, 1984). During the vegetation season, potassium is used to build up the plant's tissues (Renman, 1989); on the other

hand, potassium is released from the decaying tissues slower, than other cations, such as calcium or sodium (Brammer and Wetzel, 1984). As a result, *S. aloides* clumps depress the potassium levels compared to open water (Mulderij et al., 2009). This effect was also observed in our experiments. Brammer (1979) suggested that the planktonic chlorophyll reduction is brought about by alteration of the water ionic composition, as well as competition for nutrients. Jaworski et al. (2003) demonstrated that low potassium concentrations failed to limit the growth of two species of diatoms and one species of photosynthetic flagellates, suggesting that potassium absorption by water soldier plants is unlikely to directly influence phytoplankton growth. However, potassium concentrations may correlate with the trophic status. Potassium requirements vary among different groups of algae (Gerloff and Fishbeck, 1969). We found appreciable numbers of the diatoms in the periphyton in the planted microcosms. At the same time, significant concentrations of Chl *c* typical of diatoms were found in plankton samples, suggesting importance of those algae in phytoplankton as well. In the presence of water soldier, cyanobacterial numbers in periphyton were significantly lower compared to the controls. Toporowska et al. (2008) indicated seasonal changes in relative abundance of cyanobacteria in *S. aloides* periphyton: cyano-bacteria were more abundant in spring, compared to summer and fall. Diatoms dominated water soldier periphyton in all seasons, showing greater species richness (77 species total) compared to periphytom of other plants investigated.

Several studies (Mulderij et al., 2006; Strzałek and Koperski, 2009) have shown that algal biomass is reduced in the presence of water soldier even the nutrients are not limited and the light is sufficient. It is recognized that, *S. aloides* produces strong allelopathic effects upon planktonic and periphytic algae (Jasser, 1995; Mulderij et al., 2005; Hilt, 2006; Mohamed and Al-Shehri, 2010); however, published reports on how different algae respond to the plant are contradictory. Different strains of the same

species of algae may differently respond to the chemicals produced by water soldier (Mulderij et al., 2005; Al-Shehri, 2010). The majority of works studied only the influence of plant extracts; however such approach reflects only potential effects. Less researchers studied effects of plant exudates. The latter approach is more correct since the metabolites of live plants particularly may really change the dynamics of some species and structure of aquatic communities. Although there is little doubt about allelopathic influence of plant upon the algal community, the exact mechanisms and targets of such an influence remain to be identified.

Similarly, aquatic plants can repel or suppress zooplankton (Pennak, 1973; Burks et al., 2000). Our experiment detected no such influence, as zooplankton numbers, biomass, and species richness were somewhat higher in the planted microcosms compared to the controls. Similar results were obtained in *S. aloides* mats in Lake Bużysko (Strzałek and Koperski, 2009). Growth of Chydoridae, as well as *C. quadrangula* is responsible for the observed increase of cladoceran fraction among the zooplankton. Euplanktonic *D. longispina*, a dominant species in the controls, remained numerous in the planted microcosms as well. Those organisms are known to be present sporadically among *S. aloides* (Irvine et al., 1990; Strzałek and Koperski, 2009). Whereas Irvine et al. (1990) concluded that Daphnia abundance is reversely correlated with the density of *S. aloides*, other authors failed to find that relationship (Strzałek and Koperski, 2009). Although daphnias prefer open water, they may develop among water soldier plants if the conditions (including food availability) are right.

It is also unlikely that lower numbers of calanoids in the planted microcosms is due to allelopathic influence of plants. Calanoids are well-known to avoid floating and submerged plant areas (Dorgelo and Koning, 1980) which may be probably related to their locomotion manner.

We attribute the changes in the zooplankton community primarily to restructure of the

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environment (Bittel, 1980) and changes in the trophic resources. Macrophytes, suppressing phytoplankton, reorganize the classical food web and facilitate the transfer of organic material from bacteria and protozoa to the higher trophic level (to metazooplankton). The share of zooplankton in the sum plankton biomass was twice as higher in the microcosms with plants. In control, the ratios of biomasses of bacteria, phytoplankton and zooplankton were 1: 1.2: 3, respectively; in the planted microcosms, 1.5: 1: 6, respectively. This suggests the importance of dissolved organic matter recovery and reutilization at the higher trophic levels via microbial loop.

The overall bacterial numbers remained comparable between the controls and planted microcosms. This was due to a balance between the organic nutrient supply enhancement on one hand and the grazing pressure increase on the other. Bacterial growth can be stimulated by organic plant metabolites, nutrients excreted by zooplankton (Ejsmont-Karabin, 1984) and organic matter leaching from senescent plant parts (Efremov et al., 2012) and phytoplankton. At the same time, formation of the bacterial aggregates and microcolonies and association of bacteria with detrital particles indicates that bacteria are likely to have experienced substantial grazing pressure from HNF. According to Langenheder and Jürgens (2001) up to 50% of the microbial biomass may be found in the form of such aggregates under those conditions. Simultaneously, zooplankton can directly feed on larger bacterial aggregates. Thus, we hypothesize that bacteria supports a fair portion of zooplankton growth, either directly, by zooplankton feeding on bacterial aggregates, or in a less direct way, via heterotrophic flagellates (Carrik et al., 1991). The latter pathway seems to be more plausible, as protists are an important food source for zooplankton, especially when algal numbers are low (Sanders and Wickham, 1993). This link is well-established for *Daphnia* (Carrik et al., 1991, Sanders et al., 1996); it is likely that HNF serves as an important food source to *C. quadrangula* as well, since Šimek et al. (1997)

noted a significant decline in HNF in the presence of *C. quadrangula* and *Diaphanosoma brachyurum* (Liévin). Likewise, numbers of Chydoridae increased among *S. aloides* and correlated with numbers of periphytic HNF, allowing us to suggest a trophic link between HNF and Chydoridae.

Though water soldier clearly influenced the algal abundance and community composition, its effects upon the heterotrophic organisms of plankton and periphyton were limited. Species forming the zooplankton or periphyton were eurybionts, and environmental changes not were beyond limits of their tolerance. However, influence of plants on abundance of individual species and groups of heterotrophic organisms is possible, since a significant correlations with some hydrochemical parameters were detected. The present experiment proves that the maintenance of zooplankton biomass in the macrophytes may occur due to the additional support from the bacteria and protozoa. Perhaps, plant effects would be more significant at higher plant densities.

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